

Grooming Dynamics Among Captive African (*Colobus angolensis*) and Asian  
(*Trachypithecus cristatus*) Colobines

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## **ABSTRACT**

Allogrooming, or attentive manipulation of the fur or skin by other individuals, has both utilitarian and social functions. Evidence for the latter includes reciprocation of mutual grooming or alliance formation, conflict reconciliation, and social mobility in hierarchies. A large body of evidence from numerous primate taxa indicates that grooming tendencies are strongly associated with feeding competition, emigration patterns, and social structure.

In this study, I examined differences in grooming frequencies within and between one group each of captive African (*Colobus angolensis*) and Asian (*Trachypithecus cristatus*) colobines at the Columbus Zoo. Data were collected from June – August 2010 using focal sampling methods which yielded approximately 50 hours of data for each group.

Both groups are female-bonded (generally associated with strong female philopatry, kin support, and frequent female-female social behavior), and I predicted that grooming between females would be more frequent than female-male grooming in both species. However, because these species have different behavioral patterns in the wild, I predicted that there would be some differences of grooming partner preferences between these two populations (with a null hypothesis of no difference between groups). As previous research has shown a reduced amount of grooming exhibited in some wild Asian colobines, I predicted grooming frequencies would be higher in African colobus (*C. angolensis*) females than in silvered langur (*T. cristatus*) females.

Using a chi-square statistic to test significance, female-female grooming was found to be significantly higher than female-male grooming among both *T. cristatus* ( $\chi^2 = 7.166$ ,  $p = 0.007$ ) and *C. angolensis* ( $\chi^2 = 43.183$ ,  $p < 0.0005$ ). The statistically significant difference demonstrated that silvered langur females actually groomed other group members more often than Angolan colobus females ( $\chi^2 = 28.528$ ,  $p < 0.0005$ ). I conclude that the female-bondedness exhibited in wild groups of both species is pervasive in these captive populations as represented by grooming. Differences between these populations and wild groups may vary according to differential group composition and bonding, small sample sizes, and/or disparities in enclosure space.

## **INTRODUCTION & BACKGROUND**

Allogrooming, defined as attentive oral or manual manipulation of the fur or skin by another individual (Capitanio & Reite, 1984; Hutchins & Barash, 1976), is a significant aspect of primate life. While some researchers argue for its function as primarily utilitarian (Barton, 1985), others assert that its social role is more important (Dunbar, 1991). Many authors acknowledge a dual function; for example, both Hutchins and Barash (1976) and Sánchez-Villagra et al. (1998) incorporate the social benefits of allogrooming and the practicality of ectoparasite removal into their theoretical perspectives. While it is true that the hygienic benefits of allogrooming are often overlooked by socioecologists (Hutchins & Barash, 1976), there is ample evidence to suggest that grooming is a social currency that significantly impacts the lives of nonhuman primates. This is especially true for Old World monkeys and apes (Dunbar, 1991).

Hamilton (1976) established a rule that explains altruistic behavior amongst kin with an equation involving three variables: cost (c), benefit (b), and degree of relatedness (r) to the individual in need. As long as the product of relatedness and benefits outweighs the cost ( $c < br$ ), it is worth it for an individual to behave altruistically toward another. In a classic example of this, Kurland (1977) showed that Japanese macaque grooming frequencies positively correlated with relatedness. Seyfarth and Cheney (1984), however, demonstrated that this type of bondedness is not limited to relatedness. When individuals in group living form strong associations with each other through bonding behaviors like grooming, they can procure a certain amount of support from their partners (e.g. in predator defense situations).

Throughout the primate order, allogrooming is the most universal social behavior (Seyfarth & Cheney, 1984), although there can be substantial differences between populations of the same species (Sánchez-Villagra et al., 1998). Social structure is defined as the *interactions*

between individuals, the *relationships* these reflect (through their patterning, content and quality), and the *structure* of those relationships (Hinde, 1976; Seyfarth, 1977). Due to an individual's utilization of a particular social structure as a means to obtain food, avoid predators, and acquire mates (van Schaik & van Hooft, 1983), each type of social structure should correlate with particular grooming frequencies and partner preferences (Dunbar, 1991; Hinde, 1976).

Examples of social structures include noyau (e.g. prosimians and orangutans, in which the home ranges of males overlap with multiple females' territories), polygyny with multi-male or one-male units (e.g. colobines), fission-fusion (e.g. spider monkeys and chimpanzees), polyandry (e.g. emperor tamarins), and monogamy (e.g. pygmy marmosets and gibbons). In each of these social structures, there are non-random grooming tendencies between individuals that may reflect relatedness, proximity, or bondedness. Several examples are reviewed here.

A noyau is a predominantly solitary social structure (Dagosto et al., 2001). Females and offspring in these groups interact with each other most often (Rowe, 1996), with the primary inter-individual association with others being vocalizations and olfactory communication (Crompton, 1987; Eisenberg, 1972). The infrequency of allogrooming in orangutans (van Noordwijk & van Schaik, 2009) exemplifies the scarcity of interactions in a noyau between individuals, with the major exception of females and their offspring.

Multi-male, multi-female groups contain more than one individual of both sexes. In these groups, there are often complex hierarchies and social relationships allowing for more than one reproductive male (Rowe, 1996; van Schaik & van Hooft, 1983). Macaques often manifest this type of social structure. Male emigration or "dispersal" to other populations at a certain age is common in macaque species as it is in most Old World monkey species (Cheney & Seyfarth, 1983). Emigration of males is positively associated with greater frequencies of female

involvement in grooming (e.g., Assamese macaques) in comparison to male grooming. This is because the females that remain in the group are likely related to each other. Conversely, female dispersal is usually associated with male philopatry and thus more grooming participation by males (e.g., chimpanzees; Cooper & Bernstein, 2000; Mitani, 2009). Chimpanzees and spider monkeys associate in a type of multi-male, multi-female social system called a fission-fusion society. This group type is defined by multiple sub-units that regularly unite when food is abundant enough to sustain them, but divide when food becomes scarce. For example, patterns of convergence between these smaller groups reflect low feeding competition, whereas high risk of predation precedes disengagement of them (van Schaik & van Hooff, 1983). Fission-fusion societies may also base their patterns of synthesis and division on sex, because foraging strategies can differ between males and females. Male philopatry is also found in the multi-male, multi-female groups of red colobus, and this dispersal pattern accounts for the lack of female bondedness and for the high frequency of female-male grooming (Korstjens & Sterck, 2002). In the red colobus, related males groom most often with each other.

Female-bondedness is a mechanism by which related or unrelated females can join forces to defend resources for themselves and their offspring. In societies that are female philopatric, females remain with their natal groups and defend high quality resources (Wrangham, 1980). One-male units (e.g. Asian colobines and some black-and-white colobus) are characterized by multiple reproductive females and often female philopatry, leading to female-bondedness and thus greater frequencies of female-female grooming (Kirkpatrick, 2011).

One example of a behavioral pattern within various social structures is exhibition of reciprocal grooming in exchange for approximately equal return of mutual grooming (Gomes et al., 2009; Henzi & Barrett, 1999; Manson et al., 2004). Primates also exchange allogrooming for

access to food shares (de Waal, 1997) or to reproductive access to mates (Gumert, 2007). The recruitment of conspecific support through alliance building is one particularly adaptive social utility of allogrooming. With evidence that primates form cooperative associations for future benefits (Foster et al., 2009; Kudo & Dunbar, 2001; Seyfarth & Cheney, 1984) and recognizing that grooming is an indicator of social relationships (Dunbar, 1991; Hinde, 1976), it is plausible that females may initiate supportive partnerships by grooming in order to gain future protection against aggressive outsiders (Kappeler & van Schaik, 2002). For example, when males attempt to join groups, they often display aggressive behaviors (Fedigan & Jack, 2004), especially toward previous males' offspring (Pradhan & van Schaik, 2008). In many instances, this aggression takes the form of an invading male killing the resident male's offspring. Because infanticide occurs during male takeovers, as demonstrated by many species (chimpanzees, Arcadi & Wrangham, 1999; Hanuman langurs, Borries, 1997; chacma baboons, Palombit et al., 2000; black capuchin monkeys, Ramírez-Llorens et al., & Janson, 2008; Verreaux's sifakas, Littlefield, 2010), it is in the father's interest to defend the group from attack in order to retain his tenure as resident male and ensure his reproductive fitness.

Due to findings indicating a significant positive association between infant mortality and male takeovers (van Noordwijk & van Schaik, 2001), female defense against such attacks has been proposed as an adaptive counterstrategy (Hrdy, 1979). Female primates may respond to these threats by engaging in behaviors such as grooming in an attempt to strengthen bonds with the resident males for protection (Seyfarth & Cheney, 1984). Grooming may also function to reduce antagonism within groups. All social primates, with the possible exception of ring-tailed lemurs (Kappeler, 1993), utilize reconciliatory behavior after conflicts (Arnold & Barton, 2001). Primate groups have a proclivity to restore peace following antagonistic interactions (de Waal &

Yoshihara, 1983), especially when alliances have formed within groups (Arnold & Barton, 2001; Thierry, 1990).

Social mobility within ranked hierarchies might also motivate primates to participate in allogrooming. Within the fission-fusion society of chimpanzees, related males make up the core of a chimpanzee community. These males use allogrooming to establish alliances and appease rivals within a hierarchy (Foster et al., 2009). Among multi-male, multi-female populations like tufted capuchin monkey (*Cebus apella*) societies, grooming also may function to establish social bonds and allow individuals to advance up the social ladder (Parr et al., 1997). Nevertheless, inherent kinship biases can override these endeavors (Schino et al., 2009).

As discussed above, allogrooming strongly corresponds to the structure of primate societies. This is evidenced by utilization of grooming by primates in reciprocal exchange (of mutual grooms, access to limited food resources, and reproductive access), formation of alliances to ensure protection during violent encounters (e.g. male takeovers), reconciliation of conflict within groups, and upward mobility within hierarchies.

### **Colobine Societies**

The taxonomic family Cercopithecidae within the infraorder Catarrhini contains the primates commonly referred to as Old World monkeys. These diurnal primates are larger than their New World monkey relatives in the Western Hemisphere and have one less premolar (Fleagle, 1999; Rowe, 1996). The Cercopithecidae family contains two subfamilies: the Cercopithecinae and the Colobinae. Cercopithecines eat mostly fruit and utilize cheek pouches as a means to increase foraging efficiency, while colobines eat mostly leaves, seeds, and unripe fruit (Fashing, 2011; Kirkpatrick, 2011). “Kolobos” in Greek means mutilated, for which colobines are named due to the appearance of their reduced or absent (in the African genera)

thumbs (Korstjens, 2001; Oates & Davies, 1994; Rowe, 1996). Colobines have high, razor-edged cusps on their molars that are adapted for shredding leaves (Lucas & Teaford, 1994). Because it is difficult to digest leaves, colobines have evolved a sacculated stomach that utilizes bacteria to break down tough fibers like cellulose (Fashing, 2011; Kay & Davies, 1994; Korstjens, 2001). Colobines tend to have longer hind limbs and tails than other Old World monkeys (Rowe, 1996).

Although there is considerable diversity within and between species and populations, many colobine species live in one-male units with multiple breeding females (Fashing et al., 2007; Fimbel et al., 2001; Rowe, 1996). The majority of colobine species are female philopatric (Rowe, 1996); females remain within their natal group while males eventually disperse to a non-natal group. Most colobine species are female-bonded, which is defined by Korstjens and Sterck (2002) as the combination of strong female philopatry, kin support, and frequent affiliative interactions between females.

Affiliative behaviors (Lehmann et al., 2007) like grooming, playing, courtship and mating rituals, and aggression (often accompanied by reconciliation) occur frequently in colobine societies in comparison to the closely related cercopithecines. Grooming is one of several post-conflict appeasement behaviors used by colobines (*Trachypithecus obscurus*, Arnold & Barton, 2001; *Colobus guereza*, Björnsdotter et al., 2000). These interactions tend to be directed exclusively to other individuals within rather than between groups (Newton & Dunbar, 1994). Although exceptions exist (Silk et al., 2004), it is widely recognized that related females form the core of most Old World monkey societies (Wrangham, 1980; Silk et al., 2004). Thus, as a general rule, females in female-bonded Old World monkey societies will interact with other females within their group more often than with males in their group. These interactions



include both agonistic and affiliative behaviors.

## **African Colobines**

The African colobines come in three color schemes: black-and-white, red, and olive. Various types of black-and-white colobines represent the *Colobus* genus, whereas *Procolobus* is made up of both red and olive colobines (Rowe, 1996). *Colobus* species have three chambers in their sacculated stomachs and females lack sexual swellings. Their close relatives in *Procolobus* have four-chambered stomachs, and estrous females exhibit large sexual swellings (Rowe, 1996). *Colobus* and *Procolobus* also have divergent social structures: black-and-white colobines tend to have one-male units or multi-male, multi-female populations with one dominant male (Rowe, 1996) while red colobines almost always form multi-male, multi-female groups (Korstjens, 2001; Rowe, 1996). Males are often philopatric in *Procolobus*. As a consequence, females are less likely to bond through such interactions as grooming (Korstjens & Sterck, 2002) and related males groom most often with each other. In these societies, it is more beneficial for females to invest time in grooming males than to groom each other.

Feeding competition is also an important variable to consider when trying to predict the most likely behaviors within social structures (van Schaik & van Hooff, 1983). Korstjens and Sterck (2002) examined differences between sympatric forms of each genus (*C. polykomos* and *P. badius*) and found that differences in the food distribution of their preferred diets resulted in differential food adaptations. This was a key factor leading to differences between their societies. Many colobines utilize banqueting as a foraging technique, meaning that they remain in one general area to utilize evenly distributed, abundant patches of leaves (Newton & Dunbar, 1994). Leaves tend to be more readily available than fruit or other food, allowing for relatively reduced competition for colobines. This creates less stringent hierarchies due to the reduced

feeding competition compared to more frugivorous cercopithecines. Between red and black-and-white colobus monkeys, however, there are differences in the type of feeding competition. In the Taï forest, for example, the red colobus monkeys (*P. badius*) participate in scramble competition (Korstjens & Sterck, 2002), which is defined by a smaller amount of resources that are distributed so evenly that the costs of physically competing over them outweigh the benefits (Korstjens, 2001). This latter competition is relatively less aggressive due to the inability for any one individual to dominate a patch of food. Black-and-white colobus, however, engage in contest competition, which can be intensified by the ability for individuals to control patches of coveted food (Korstjens, 2001). This is especially true when food is abundant enough for the group's sustenance but small enough for the group to defend it collectively.

Scramble competition such as that exhibited by red colobus leads to egalitarian societies. Contest competition, however, can lead to linear dominance hierarchies (Korstjens, 2001; Sterck et al., 1997). Linear dominance hierarchies call for coalitions and alliances between individuals in order to gain leverage within this competitive climate (Sterck et al., 1997). It is therefore plausible that allied confederations readily form among female kin in the female philopatric societies that call for this type of support. Just as alliances between individuals form within groups to reinforce protection in threatening situations (Seyfarth & Cheney, 1984), these same relationships can allow individuals access to food shares (de Waal, 1997). Although black-and-white colobus monkeys in the Taï forest groom less than the red colobus overall, the female philopatry of the black-and-white colobus groups (as in most Old World monkeys) is reflected in the females' tendency to be both the primary groomers and recipients of grooming (Fashing, 2011). Red colobus females, on the other hand, are unrelated and tend to groom the related males more than other females in their groups (Korstjens & Sterck, 2002).

## **Asian Colobines**

Seven genera of colobines (*Presbytis*, *Semnopithecus*, *Pygathrix*, *Nasalis*, *Simias*, *Rhinopithecus*, and *Trachypithecus*) are located in Asia. These colobines typically have a social structure of one-male units with multiple adult females (reviewed in Kirkpatrick, 2011; *Trachypithecus cristatus*, Bennett & Davies, 1994). Males disperse most of the time (although females do on occasion, and routinely in *T. phayrei*) leaving these groups (e.g. *T. cristatus*) with philopatric females (Kirkpatrick, 2011). Therefore, the core of the group consists of related females. *T. cristatus* monkeys (also known as silvered langurs) in particular have exceptionally large forestomachs and better shearing cusps on their teeth than other Asian colobines (Kirkpatrick, 2011), allowing them to digest food even more efficiently.

The evidence of female philopatry and high frequency of females' intrasexual interactions (Kirkpatrick, 2011; Rowe, 1996) support the classification of *T. cristatus* as a female-bonded species (Wrangham, 1980). While similar to their African relatives in that Asian colobine females are the primary groomers and recipients of allogrooming, the Asian genera are relatively asocial when it comes to grooming (Kirkpatrick, 2011). This is possibly an effect of a decreased amount of competition. As with African colobines, competition is not as major of a factor in the life of Asian colobines due to their ability to digest mature foliage, allowing for plentiful food resources and fewer restrictions on group size (Yeager & Kirkpatrick, 1998).

### **Colobine Grooming: This Study & Its Context**

The fact that the Columbus Zoo houses several social groups of colobine monkeys, one African and one Asian, provides an opportunity to examine grooming dynamics in greater detail. In this study, I examined comparative social behavior by collecting data on the grooming

frequencies in one African (*C. angolensis*, or the Angolan colobus) and one Asian (*T. cristatus*, or the silvered langur) colobine.

Both African and Asian colobines benefit from the low-energy digestion of a primarily folivorous diet. These monkeys utilize sacculated stomachs to process food that many animals cannot (Bennett & Davies, 1994; Oates, 1994). Unlike black-and-white colobines' lack of sexual swellings, females in *T. cristatus* have unexaggerated genital swellings that do not seem to have a significant effect upon fertility or sexual behavior (Shelmidine et al., 2007). Another difference between the two focus groups concerns thumb morphology; Asian colobines (e.g. *T. cristatus*) have reduced yet existent thumbs, while African colobines (e.g. *C. angolensis*) lack thumbs. This difference could result in less adept grooming techniques in African colobines (Hutchins & Barash, 1976).

As discussed earlier, colobine species are often formed in one-male units or in multi-male, multi-female populations with one primary dominant male (Fashing et al., 2007; Fimbel et al., 2001; Rowe, 1996). Both *T. cristatus* and *C. angolensis* have adapted to these social structures with female philopatry and frequent female-female interactions, but it is possible that the feeding competition of black-and-white colobus in comparison with the minimal competition for resources in *T. cristatus* could lead to between-species differences in their social behavior. Although the zoo setting minimizes the need for feeding competition and predator defense, many years of selecting for behaviors associated with these phenomena in the wild should result in the behaviors being encoded in the genome. We therefore shall expect similar affiliative patterns in captivity.

Recognizing the fact that grooming can reliably illustrate social structure and social dynamics, I tested hypotheses related to the frequency of grooming by adult females. I hypothesized the following:

- 1.) The ratio between grooming bouts and non-grooming bouts between female Angolan colobus (*C. angolensis*) and other females in their group will be higher than the ratio between females and the adult male. Female-bonded groups tend to have this pattern in the wild, and this behavior should be maintained in captivity.
- 2.) Similarly, the ratio between grooming bouts and non-grooming bouts between the Asian colobines (*T. cristatus* or silvered langurs) and other females in their group will be higher than the ratio between females and the adult male. This species is also female-bonded.
- 3.) The ratio between grooming bouts and non-grooming bouts will be greater between *C. angolensis* than in *T. cristatus* due to the typically reduced amount or lack of grooming exhibited in wild Asian colobines.

## **MATERIALS & METHODS**

I compared the grooming frequencies of both species. The analyses focused specifically upon occurrences of female-female grooms versus female-male grooms. For each individual, differential amounts of 5-minute-blocks were observed. Each individual's frequency has been calculated into proportions in order to avoid obscuring data due to biased amounts of time watched.

### **Study Groups**

All data were collected from captive groups of silvered langurs (*T. cristatus*) and black-and-white colobus (*C. angolensis*) housed at the Columbus Zoo and Aquarium in Columbus,

Ohio, between 17 June and 27 August 2010. Individuals in each group were identified using tail features, including color and shape, as well as facial traits. Other characteristics were used in identification when possible, including size differences for juveniles and elongated nipples for mothers in the langur group.

The silvered langur group was comprised of seven individuals including one adult male (Digby, age 6 at the outset of the study), an adult female related to the adult male (Eggnog, age 5), two unrelated adult females (Patty and Gumby, ages 10 and 9, respectively), and three juvenile males (Pokey, Ollie, and Fernando, ages 2 years, 22.3 months, and 11.4 months, respectively; Table 1). A female juvenile was born to Gumby on 23 August. Digby is the sire of all four juveniles. Gumby is the mother of Pokey, Ollie, and infant, and Patty is the mother of Fernando (Figure 1). Patty was also pregnant during this study, but she did not give birth until after the study had concluded.

The Angolan colobus group was composed of four individuals including one unrelated adult male (Sasha, age 9 at the beginning of the study), one adult female (Tina, age 14), and two juvenile females (Olivia and Chacka, aged 35 months and 23 months; Table 2). Tina is the mother of both Olivia and Chacka (Figure 2). Sasha was introduced to the females on 17 June.

### **Study Sites**

The entire langur exhibit includes two indoor enclosures (left and right) with part of the exhibit outdoors. Doors with latches are available for monkeys to move between exhibits when keepers permit. A bachelor group of older juvenile and adult males shares these exhibits with the focus group of *T. cristatus*, but reproductive and bachelor groups are kept separated at all times.

The focus group is allowed to move between the indoor and outdoor enclosures on

specified days. Due to difficulty identifying this group in the outdoor exhibit, however, data were primarily collected on days this group was scheduled to spend time inside. The indoor exhibit has dependable visibility from the viewing area, which is separated from the enclosure by a glass wall (Figure 3). The enclosure consists of a stone floor with vertical steps, providing keepers with a means for mobility within all parts of the enclosure. Substrates include a ladder, several connected pipes or scaffolding, synthetic vines, and a few food and water bins. There are also two large pillars made of stone.

The black-and-white colobus exhibit is an outdoor enclosure. The interior is only visible to guests through a small window, but it provides insufficient visibility for observation. At no time are these monkeys allowed to move freely between the inside and outside areas. This exhibit has dependable visibility from catwalks outside and from a shelter, with netting separating guests from monkeys for the former and a pane of glass functioning this way in the latter. This outdoor enclosure includes three synthetic trees of varying sizes, one of which limits visibility if monkeys sit atop it. Other landmarks include four horizontal platforms upon which monkeys can sit or lounge (Figure 4), one freestanding wooden pole, a few synthetic vines, and two synthetic stumps. Horizontal crossbeams are available for individuals to commute between most of the landmarks. There is also space available beneath each of the four platforms where monkeys can rest. Five buckets specified for either food or water are available for monkeys to forage.

### **Data Collection**

Beginning 17 June 2010, data collection was conducted between the hours of 12:00 and 19:00. One exception to this rule was a five-hour day of Angolan colobus data collection beginning at 10:15 AM. Data were collected in blocks that averaged 3.9 hours for both species,

totaling 50 hours per species. Data were collected using instantaneous focal sampling (Altman, 1974). Within five-minute intervals, focal individuals were sampled for the nature, substrate, participants, and frequencies of affiliative interactions and other behaviors at the beginning of every minute. During the last three days of data collection, I recorded alloparenting activities by individuals pertaining to Gumby's infant (e.g. holding, passing, and nursing).

Proximity as a measure of bonding behavior (Korstjens, 2001; Kudo & Dunbar, 2001) was also recorded at the beginning of each five-minute sampling interval. All individuals within one meter, within three meters, within five meters, and beyond five meters of the focal individual were recorded (Table 3). In order to control for temporal autocorrelation of samples between focal individuals, alternating blocks of time were removed for each species. Remaining observational data included 25.1 hours for the silvered langurs and 24.9 hours for the Angolan colobus.

Eight categories of behavior were recorded:

1. **Allogrooming** – attentive maintenance of fur or skin by another individual
2. **Self-grooming** – attentive maintenance of one's own fur or skin (scratching included but differentiated)
3. **Social** – any non-grooming interactions, e.g. playing or aggressive behavior
4. **Consumption** – activities associated with foraging or eating (drinking included but differentiated)
5. **Nursing** – offspring (infants or juveniles) breast-feeding from mothers
6. **Resting** – inactivity (including sleeping, sunbathing, and general immobility)
7. **Moving** – individuals moving within enclosure (walking, running, and climbing)
8. **Visitor** interaction – contact with visitors (taking leaves from guests through netting, responding to visitors' actions in general)



The chi-square statistic was used to test differences in grooming frequencies by females. Targets of grooming included in analyses of each group consisted of 1.) the adult male and 2.) other females. The female infant born to Gumby near the end of the study was excluded from any analysis. These statistical analyses compared the frequency of grooming bouts to the frequency of total bouts watched (both grooming and non-grooming) for each combination of female/other female and female/adult male to test significance greater than chance.

## **RESULTS**

Table 4 indicates the frequencies by which females in each group groomed other females. Table 5 presents data on the frequencies that females in each group groomed the adult male. Chi-square statistics were run through SPSS 17.0 for Macintosh with  $\alpha$  set at 0.05.

In the silvered langur group, there were three females: Gumby, Egnog, and Patty. Gumby and Egnog groomed other females for 19 percent and 15 percent, respectively, of the amount of time each was observed. Patty groomed other females for seven percent of the time she was the focal individual. Egnog groomed the adult male (Digby) more than the other females, which was for eight percent of her focal samples. Gumby groomed Digby for two percent of the time she was observed, and Patty never groomed him. In the Angolan colobus group, there were also three females. These females groomed other females at similar proportions when compared to the amount of time each was watched (Tina, 20%; Chacka, 14%; Olivia, 21%). Of all three Angolan colobus females, Olivia groomed the adult male (Sasha) the most (1%). The other two females in this group never groomed the adult male.

I predicted that females would groom each other more often than they would groom the adult male in both groups. Female-female grooming was found to be significantly higher than female-male grooming among both *T. cristatus* ( $\chi^2 = 7.166$ ,  $p = 0.007$ ) and *C. angolensis* ( $\chi^2 =$

43.183,  $p < 0.0005$ ). I also hypothesized that the Angolan colobus females would groom other group members more often than the Asian colobine (silvered langur) females would groom others in their group. In comparing between-species female grooming of others, a statistically significant difference was found demonstrating that silvered langur females actually groomed others more often than Angolan colobus females ( $\chi^2 = 28.528$ ,  $p < 0.0005$ ).

## **SUMMARY & CONCLUSIONS**

- 1.) My predictions that female-female grooming would be significantly higher than female-male grooming in both of these captive populations was supported.
- 2.) Between species, a statistically significant difference was found indicating that silvered langur females groom others in their group more often than Angolan colobus females.
- 3.) The hypothesis that Angolan colobus females would groom others more often than silvered langur females was rejected. One possible explanation is that there are behavioral differences between captive and wild species. Enclosure characteristics and group compositions more similar to the wild would be ideal. Additionally, this comparison of colobine species may have been strengthened if the groups had bonded for more similar amounts of time.

## **DISCUSSION**

Food distribution is an important factor in the lives of primates (van Schaik & van Hooff, 1983), as it has an effect on foraging behavior and competition both within and between groups. Colobines' specialized stomachs and teeth are designed to break down leaves efficiently. These monkeys' use of banqueting (remaining in one general area to utilize plentiful patches of leaves) as a foraging technique reflects the wide distribution and ubiquity of their food resources. Monkeys in this subfamily utilize efficient digestive systems to budget their time and remain

relatively immobile, allowing the reduction of heat loss and thus the conservation of energy (Bennett & Davies, 1994). Both African and Asian colobine radiations are known for their lethargic energy (Fashing, 2011; Kirkpatrick, 2011). In this study, silvered langurs rested (defined by immobility, awake or sleeping) 70 percent of the time while Angolan colobines rested during 93 percent of their focal samples. These data underscore the general inactivity of colobines, although these percentages may be inflated due to the confined nature of life in captivity.

Females may bond with each other to recruit social support regardless of relatedness (Seyfarth & Cheney, 1984) in order to balance their access to food, protection in agonistic situations, and reproductive fitness (van Schaik & van Hooff, 1983). As a consequence of female philopatry, female colobines of both the Asian and African radiations (except for red colobus, Korstjens & Sterck, 2002) spend most of their time grooming other females within their group. This is possibly a result of their relatedness to each other, as both study groups have familial bonds amongst several individuals; kinship bonding is often a positive biasing factor in social interactions (Crook, 1966; Schino et al., 2009). The *T. cristatus* females, however, are the only completely unrelated individuals in the group. Thus, although difficult to disentangle causal factors in the relatedness and bondedness of females in the Angolan colobus (*C. angolensis*) group, the unrelated silvered langur (*T. cristatus*) females grooming each other significantly more often than males is a robust indication of female bondedness.

Although captivity minimizes competition due to provisioning of food and a lack of predators, behavioral patterns should be maintained in these species as a result of repeated selection for particular social interactions in the wild and a derived combination of genes reflecting these behaviors. Female-bondedness in both species predicts regular affiliative

behavior between females, and this was found to be true in these captive groups. The greater amount of affiliative behavior exhibited in wild black-and-white colobine populations relative to Asian colobines should have resulted in a similar pattern in captivity. Contrary to this prediction, silvered langur females groomed other group members more often than Angolan colobus females groomed others. This is possibly a product of a convenience sample within a captive setting. As discussed in Henzi and Barrett (1999), zoos have the luxury of control and visibility in comparison to field studies. Unfortunately, however, the populations are not formed in a natural manner that is necessarily affected by social interactions between individuals. Also, there was no control in the between-species variability of the enclosures. Although exact measurements of these are not available, the black-and-white colobus exhibit arguably has significant horizontal space whereas the silvered langur exhibit utilized more vertical space. This could possibly have had an effect on grooming frequencies, as the silvered langur exhibit did now allow for as much separation from other individuals. Preferences for particular substrates (either lower or higher in the enclosure) may have narrowed the proximity between individuals in the silvered langur group, in effect causing greater grooming frequencies in this particular captive population (as in Kurland, 1977). Additional data on substrate and location preferences in addition to exact horizontal and vertical measurements of each exhibit could allow for more comparable species analyses.

Group compositions in captivity are also very specific to each zoo's access to newcomers and ability to provide space. Both groups had a majority of related individuals, possibly confounding data about female-bondedness due to an explanation of kin-selected altruism (Hamilton, 1964; Kurland, 1977). On the other hand, bondedness is not limited to relatedness (Seyfarth & Cheney, 1984). Although a confound of relatedness possibly extended to both

species, the only completely unrelated individuals in the silvered langur group were the adult females. The male black-and-white colobus (Sasha) was not related to any other individuals and was new to the exhibit at the onset of the study. This novelty can possibly explicate the largely absent male-directed grooming from females in this population. In contrast, some of the silvered langurs have been together for an extended period that may have allowed for more bonding. All adults in the silvered langurs were born at the Bronx Zoo and presumably spent at least some of their time together there before reuniting at their current location. Digby and Gumby both arrived in June 2006, with Eggnog and Patty joining them in March 2008. The importance of time investment in bonding is clear in the fact that the female-female grooming rates in this group are high despite their unrelatedness. On the other hand, the highest rate of female-male grooming in the silvered langurs was found between brother (Digby) and half-sister (Eggnog), possibly indicating a remaining kinship bias.

### **Implications and Future Work**

Zoos often promote conservation through programs that provide a nurturing environment for reproductive efforts. This often means that the animals found in zoos are in captivity for protection from extinction and for a controlled environment to propagate species. Both species in this study are in the “lower risk” categories of endangerment (Rowe, 1996), but this is a relative comparison to the primates that are at greater risks. The continual categorization of colobines at increasing levels of endangerment risk is disquieting. For example, two African colobines and six Asian colobines have been listed as being critically endangered and in the top 25 most endangered primates in the world (Mittermeier et al., 2009). This also means that the wild populations are dwindling, leaving researchers with only so much time before mass extinction. Especially with species that live in dense forests, focal surveying is already difficult.

For example, most of the behavioral observations of *T. cristatus* have been done at the edge of their habitats (Bennett & Davies, 1994), which has possibly skewed the data. These limitations call for greater conservation efforts to keep these wild populations from going extinct and for more data collection on those species before it is too late (Fashing, 2007).

Together with the control provided by studies in captivity, field studies can bolster behavioral data by utilizing larger sample sizes. Wild data collection on these taxa could also help strengthen conclusions about grooming frequencies between these and other related species. Field studies could also further an understanding of the ramifications or lack thereof that captivity has on colobine social behavior. Studies in both captivity and in the wild could be utilized to correlate sexual and grooming behaviors. Collected *ad libitum* during focal samples, silvered langur male-female pairs were observed to mutually groom before copulations. Without the frequency of male-female grooms in the Angolan colobus population, this behavior was not observed. When Olivia did groom Sasha, however, she presented her hindquarters to him as if to ask for permission before grooming him. The correlation between nursing and grooming behaviors could also be examined, although if found could possibly be a simple consequence of proximity between mothers and offspring. In addition to these studies, more attention could be paid to specific degrees of genetic relatedness between individuals in order to test the effects of kinship altruism in both captive and wild populations of these species.

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## **FIGURES & TABLES**

<b>Name</b>	<b>Sex</b>	<b>Birth date</b>	<b>Age (months)</b>	<b>Relationships to others</b>
Patty	F	12/1/1999	126.5	Mother of Fernando
Gumby	F	4/16/2001	110	Mother of Ollie and Pokey
Digby	M	3/13/2004	75.1	Sire of Fernando, Ollie, and Pokey
Eggnog	F	1/10/2005	65.2	Sister of Digby
Pokey	M	7/7/2007	35.4	Offspring of Digby and Gumby
Ollie	M	8/8/2008	22.3	Offspring of Digby and Gumby
Fernando	M	7/6/2009	11.4	Offspring of Digby and Patty

Table 1: The Columbus Zoo reproductive group of silvered langurs (*T. cristatus*) with names and ages (in months) at beginning of study (17 June 2010). Infant born at end of study has been excluded, but is the offspring of Digby and Gumby and born on 8/23/2010.

<b>Name</b>	<b>Sex</b>	<b>Birth date</b>	<b>Age (months)</b>	<b>Relationships to others</b>
Tina	F	12/22/1995	173.8	Mother of Olivia and Chacka
Sasha	M	10/14/2000	116.1	Unrelated
Olivia	F	7/18/2007	35	Offspring of Tina
Chacka	F	7/12/2008	23	Offspring of Tina

Table 2: The Columbus Zoo group of Angolan colobus (*C. angolensis*) with names and ages (in months) at beginning of study (17 June 2010).



Individual	Time	Activity	Substrate	Notes
<b>Proximity Scan:</b> t0 C; 1m O; B5m S				
<b>Tina</b>	12:51	R	PL2	N/A
<b>Tina</b>	12:52	R	PL2	N/A
<b>Tina</b>	12:53	R	PL2	N/A
<b>Tina</b>	12:54	R	PL2	N/A
<b>Tina</b>	12:55	R	PL2	N/A

Table 3: Sample sheet of data collection for one individual's (*C. angolensis*) five-minute focal sample. Data for *T. cristatus* collected in same manner.

<b>Silvered Langurs</b>	<b># Grooming Bouts</b>	<b># Non-Grooming Bouts</b>	<b>Total # Bouts watched</b>
Patty -> Gumby	2	42	45
Patty -> Eggnog	1		
Eggnog -> Gumby	4	34	40
Eggnog -> Patty	2		
Gumby -> Eggnog	3	34	42
Gumby -> Patty	5		
<b>Total</b>	<b>17</b>	<b>110</b>	<b>127</b>

<b>Angolan Colobus</b>	<b># Grooming Bouts</b>	<b># Non-Grooming Bouts</b>	<b>Total # Bouts watched</b>
Tina -> Olivia	8	61	76
Tina -> Chacka	7		
Chacka -> Olivia	1	65	76
Chacka -> Tina	10		
Olivia -> Chacka	5	59	75
Olivia -> Tina	11		
<b>Total</b>	<b>42</b>	<b>185</b>	<b>227</b>

Table 4: Frequencies that females in each group groomed other females. Data in fourth column indicate total number of 5-minute bouts watched (e.g. Patty was watched for 45 total 5-minute intervals). These data were then used to form a proportion over which the ratio of grooming and non-grooming bouts could be compared.

<b>Silvered Langurs</b>	<b># Grooming Bouts</b>	<b># Non-Grooming Bouts</b>	<b>Total # Bouts watched</b>
Patty -> Digby	0	45	45
Gumby -> Digby	1	41	42
Eggnog -> Digby	4	36	40
<b>Total</b>	<b>5</b>	<b>122</b>	<b>127</b>

<b>Angolan Colobus</b>	<b># Grooming Bouts</b>	<b># Non-Grooming Bouts</b>	<b>Total # Bouts watched</b>
Tina -> Sasha	0	76	76
Olivia -> Sasha	1	74	75
Chacka -> Sasha	0	76	76
<b>Total</b>	<b>1</b>	<b>226</b>	<b>227</b>

Table 5: Frequencies that females in each group groomed their adult male. Data in fourth column indicate total number of 5-minute bouts watched (e.g. Patty was watched for 45 total 5-minute intervals). These data were then used to form a proportion over which the ratio of grooming and non-grooming bouts could be compared.

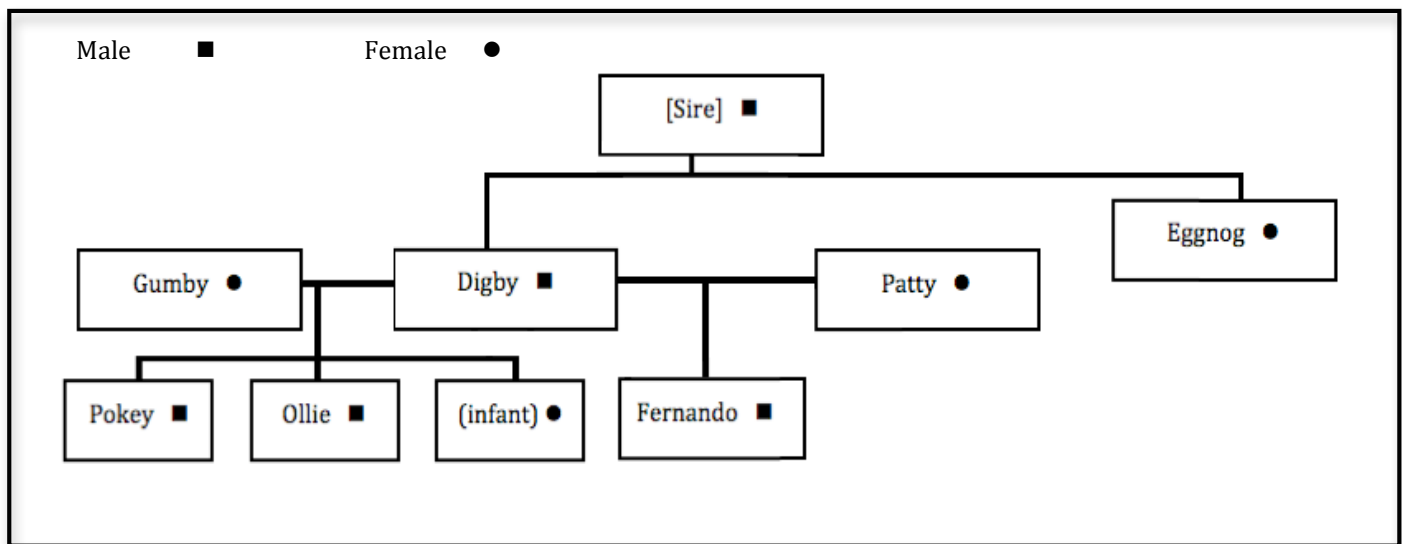


Figure 1: Silvered langur (*T. cristatus*) family tree showing relationships between individuals. Digby and Eggnog shared a sire but not a dam, so these individuals are half-siblings. Sire of Eggnog and Digby unknown to study and never at this location. Infant born to Gumby at end of study included here but excluded from analyses.

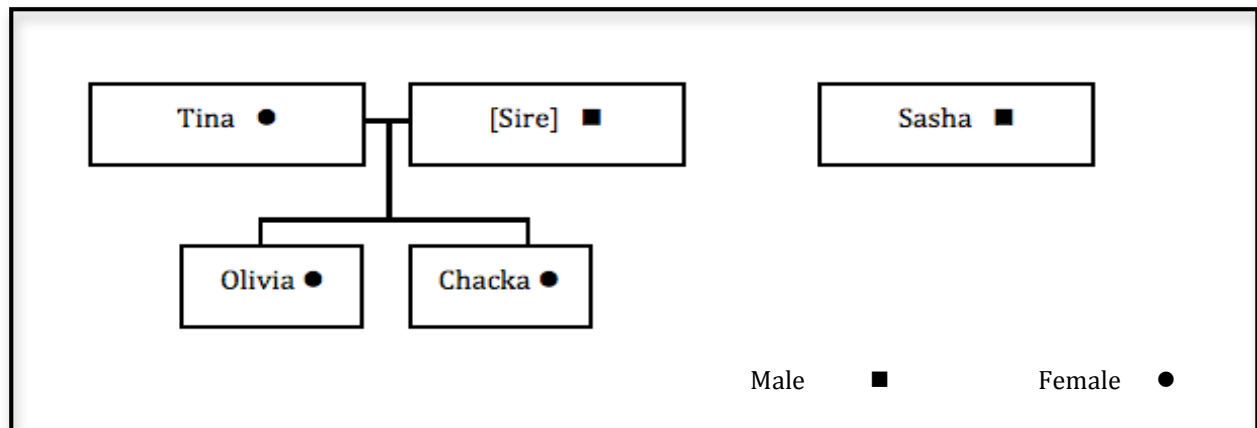


Figure 2: Angolan colobus (*C. angolensis*) family tree showing relationships (or lack there of, e.g. Sasha) between individuals. Sire was transferred from zoo before study began.



Figure 3: Left side of indoor langur exhibit. In the foreground, scaffolding and synthetic vines are visible through the glass. One of the large pillars can be seen in the background on the left.



Figure 4: Horizontal platforms often utilized for resting in Angolan colobus exhibit. Synthetic vines leading to the platforms can be seen in the foreground, as well as food and water buckets on the lower platform level.

### Frequency of Female-Female vs. Female-Male Grooms in Silvered Langurs

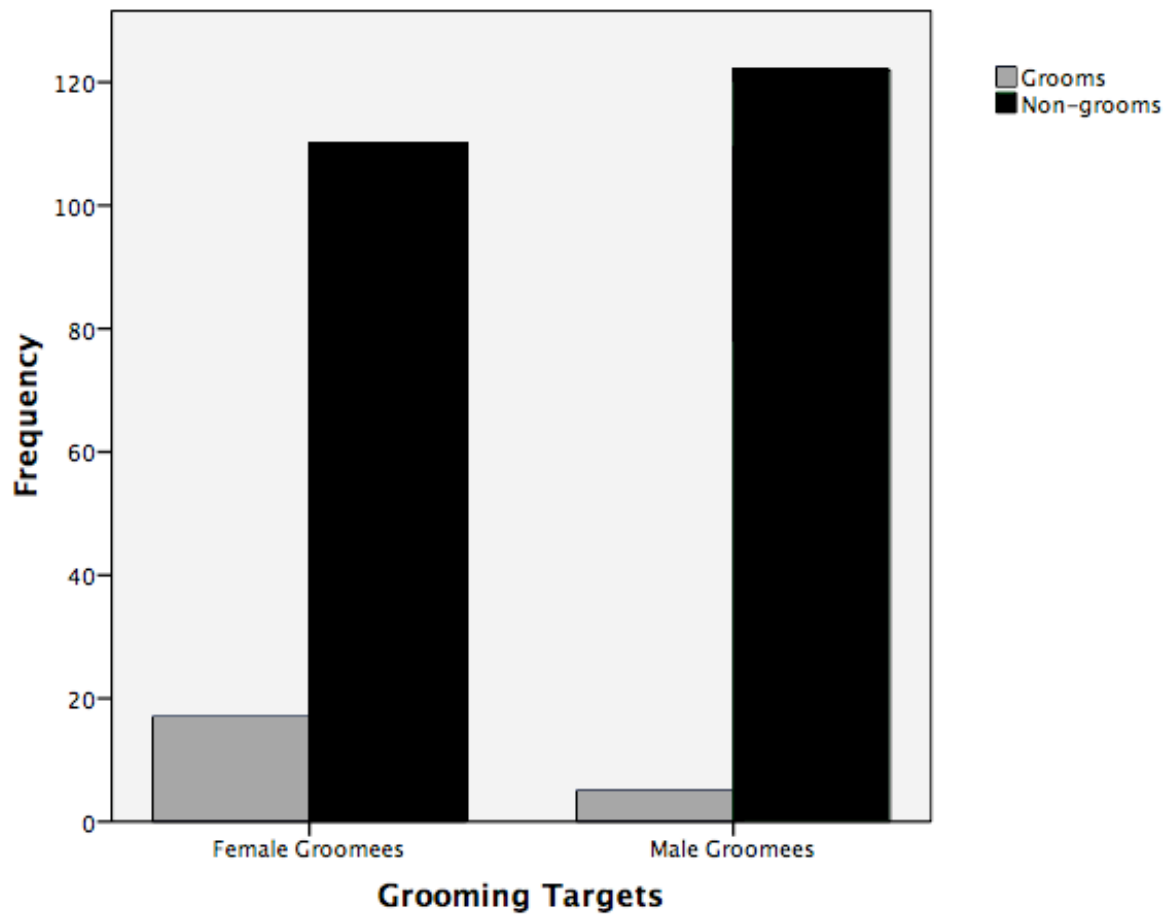


Figure 5: Silvered langur (*Trachypithecus cristatus*) female-female versus female-male grooming bouts. It was more common for *T. cristatus* females to spend time grooming other females than for them to devote time to grooming the adult male ( $\chi^2 = 7.166$ ,  $p = 0.007$ ).



### Frequency of Female-Female vs. Female-Male Grooms in Angolan Colobus

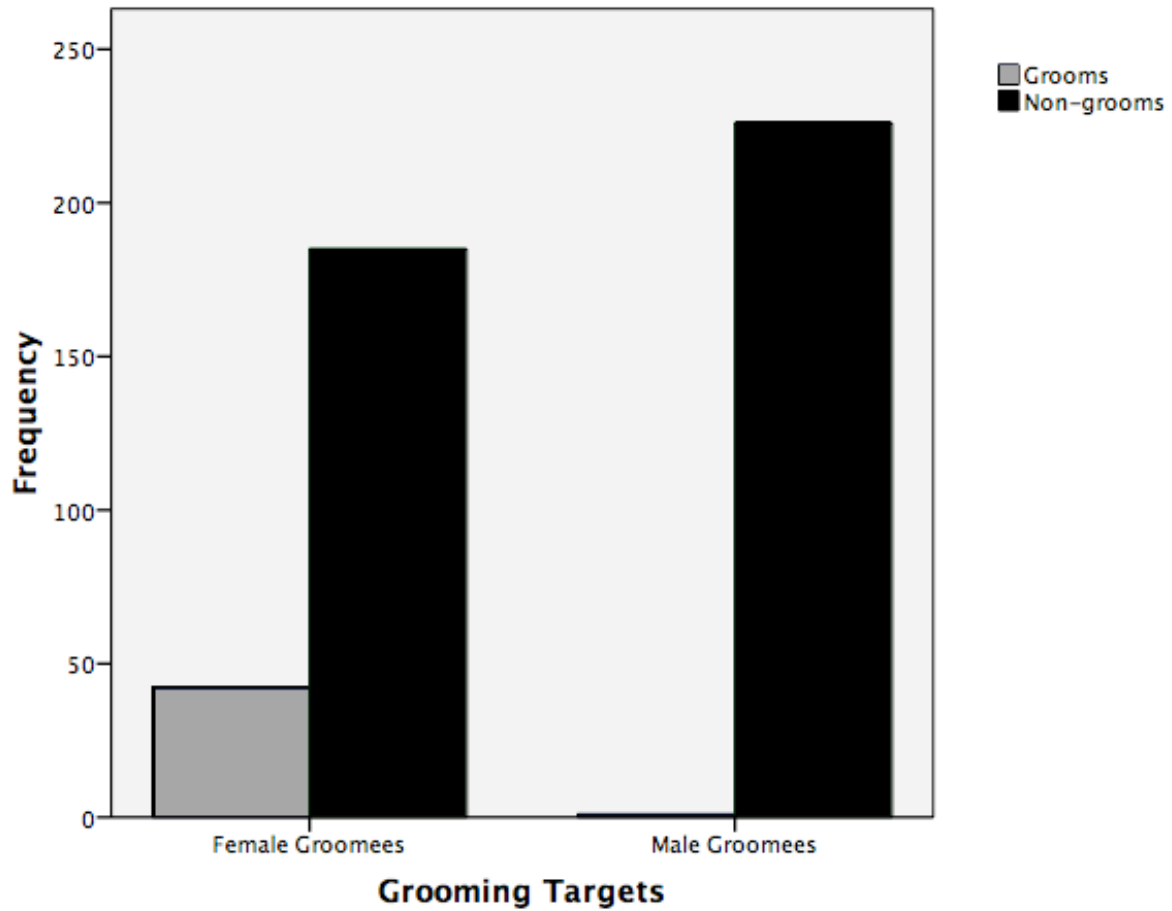


Figure 6: Angolan colobus (*Colobus angolensis*) female-female versus female-male grooming bouts. *C. angolensis* females were significantly more likely to devote grooming time to other females than to the adult male ( $\chi^2 = 43.183$ ,  $p < 0.0005$ ).

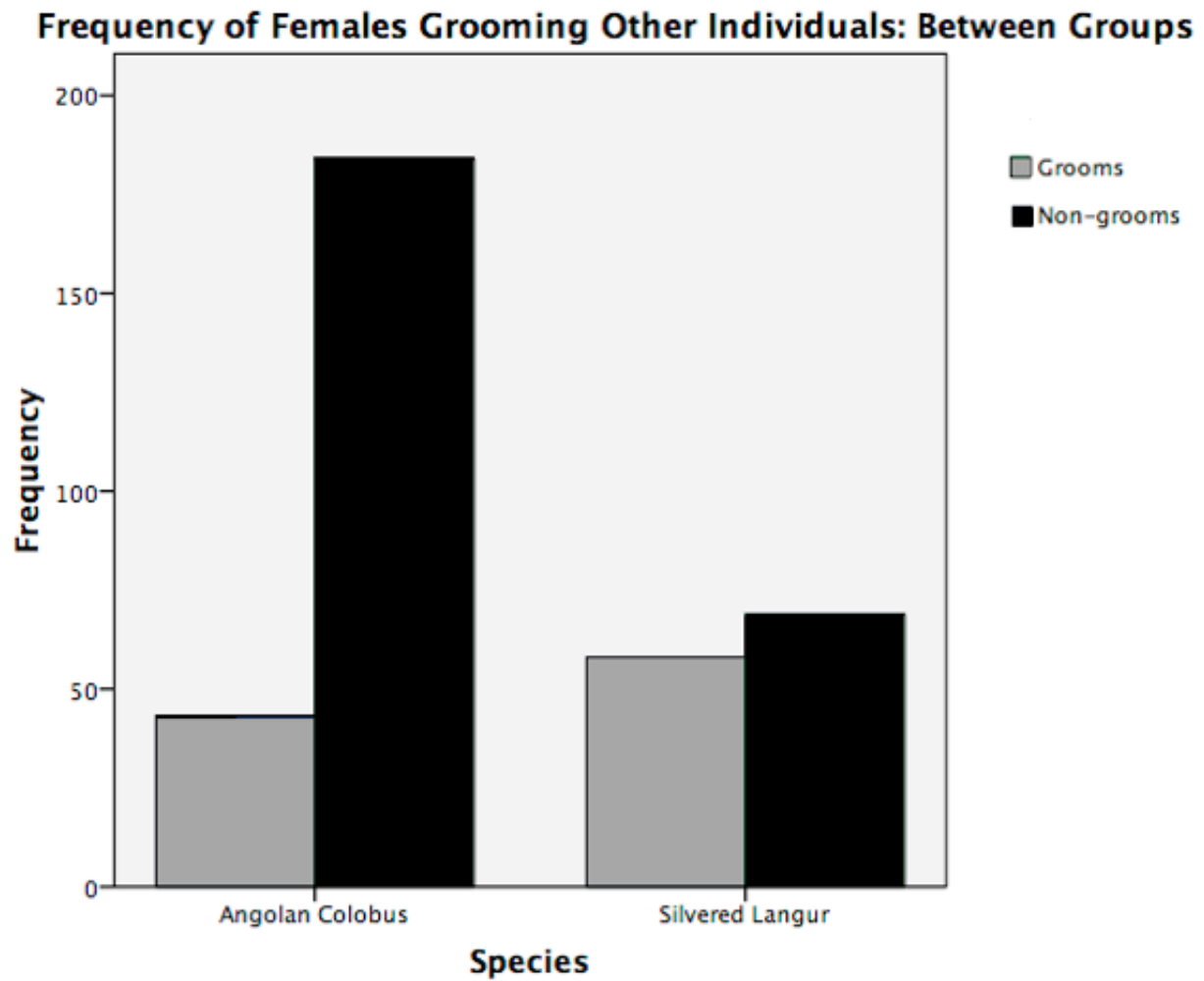


Figure 7: Between-groups comparisons of the frequencies that females groomed others. A statistically significant difference was found demonstrating that silvered langur (*Trachypithecus cristatus*) females groom others more frequently than Angolan colobus (*Colobus angolensis*) females ( $\chi^2 = 28.528$ ,  $p < 0.0005$ ).